Influence of congeneric intruder size, color, and species on *Stegastes fuscus* territory defense

Marc N. Conte

Abstract: To secure resources within coral reef ecosystems, some species within the damselfish family (Pomacentridae) actively defend territories. The juveniles of these territorial species have distinct coloration patterns, which are lost when the individuals mature. I studied the territory defense of the dusky damselfish, *Stegastes fuscus*, and hypothesized that defense would be affected by the color (juvenile or adult), size (small or large), and species (dusky or threespot) of damselfish intruders. I used models to represent size and color combinations that do not naturally occur (e.g., large individuals with juvenile coloration). I found a significant interaction between the effects of intruder size and color on territorial defense, with adult coloration increasing the response to large intruders. This effect could be because focal fish recognized adults as competitors, and juvenile coloration and size was enough to signal that an intruder was not a threat, or could be a result of the influence of intruder behavior on territorial defense. Future studies could further isolate the effects of color by only using models for each intruder type and could observe behavior of other focal species to see if the effects of juvenile coloration hold across damselfish species.

Key Words: dusky damselfish, threespot damselfish, juvenile coloration, Pomacentridae

Introduction

Coral reefs are home to a variety of fish species that coexist by partitioning resources and exploiting the wide range of niches available in these productive ecosystems. Due to the vast diversity of reef fish, there is intense competition for resources both among species and individuals. Many species within the damselfish family (Pomacentridae) maintain their place in reef ecosystems by rigorously defending choice territories from intruders. One such species is the dusky damselfish, *Stegastes fuscus*. Although within this species, individuals can choose territories for shelter from predators or nest sites, the principal function of these territories is to protect food resources in the form of algal mats (Robertson et al. 1981, Ebersole 1985).

Dusky damselfish, like other territorial species in the family, exhibit dramatically different color patterns throughout their lifespan. Juveniles are brightly colored, while the adults are almost uniformly dark brown to black except during the mating season. The benefit of this intense juvenile coloration pattern is currently unknown, although it has been suggested that the bright colors make them recognizable to adult conspecifics and thus protect them from the aggressive responses of these adults or that juveniles and adults do not overlap spatially (Deloach 1999).

Both the dusky damselfish and the threespot damselfish (*Stegastes planifrons*) are found in Discovery Bay, Jamaica and are known to be pugnacious territory defenders (Humann 1997). Both species have brightly colored juveniles with very different interspecific patterns. To explore the potential benefits of juvenile coloration and the interspecific difference in aggressive response, I hypothesized that the territorial defense of adult dusky damselfish would be affected by the size, color, and species of intruding fish. I predicted that there would be a greater aggressive response to large, conspecific individuals with adult coloration relative to the respective alternatives.

Methods

I observed territory defense in dusky

damselfish individuals on 6 – 9 March 2000. Nine focal fish were randomly selected from the rocks 20 m NW of the Discovery Bay Marine Laboratory boat ramp. I presented each of the focal fish with eight different intruders in a random order. Intruders were either live fish or models and tested the effects of size (large vs. small), color (adult vs. juvenile) and species (*S. fuscus* vs. *S planifrons*) in a completely crossed experimental design. Large intruders ranged from 12 - 15 cm and small intruders ranged from 4 - 6 cm. Buoyant laminated paper models were used to represent size and color combinations that are not naturally available (e.g., small fish with adult dusky color, small fish with adult threespot color, large fish with juvenile dusky color and large fish with juvenile threespot color), while live fish were used in all other cases.

All intruders, both live fish and models, were introduced into the focal fish territory inside a clear plastic bag. The bag was tied closed with string and weighted with either a pair of two-inch iron bolts or a single four-inch bolt. I placed each experimental intruder in the same relative position within the focal fish territory. After a 30 s period of acclimation to the experimental setup, I recorded the number of approaches made by the focal fish toward the intruder within a 4 min period. Approaches were assumed to represent defensive behavior and varied from investigation to, more rarely, overt attacks. I log-transformed the numbers of approaches to achieve normality and equal variances.

To control for the behavioral effects of intruders, I presented an adult-sized model with adult dusky coloration to six of the nine focal fish, which enabled me to compare the effect of the model with the effect of a live dusky adult on focal fish response. I also presented an empty plastic bag weighted with a pair of two-inch bolts to three focal fish as a control for the method of intruder presentation.

I used a three-way ANOVA to compare the effects of size, color, species, and all interactions on territory defense. Because neither species nor any interactions involving species were significant, I used a two-way ANOVA to compare the effects of size, color, and the size by color interaction on territory defense. I then used an orthogonal contrast within interactions. I tested the difference in response to the live and model adult dusky using a Student's t-test. I used an ANOVA to compare the effects of juvenile dusky and juvenile threespot coloration of small intruders on territorial defense. Among large models, I used another ANOVA to compare the effect of juvenile dusky or adult dusky coloration on territorial defense of focal fish.

Results

A three-way ANOVA testing the effects of size, color, species, and all their interactions showed no significant effect of species ($F_{1,71} = 0.02$, $p = 0.89$) or of any interactions involving species (all p's > 0.10). Accordingly, I chose to analyze the data in the context of the two-way ANOVA involving only size and color. There was a significant interaction between size and color on the defense response of the focal fish (Table 1). Orthogonal contrasts showed that juvenile coloration decreased the response to large intruders, but did not affect the response to small intruders (Fig. 1).

There was no difference in the response to large models with juvenile coloration as

Table 1. Effects of damselfish intruder size and color on the territory defense by focal dusky damselfish individuals.

Source	DF	MS	F	p
Size	1	0.46	4.20	0.044
Color	1	1.39	12.74	0.001
SizexColor	1	3.22	29.56	<0.001
Error	68	7.40		

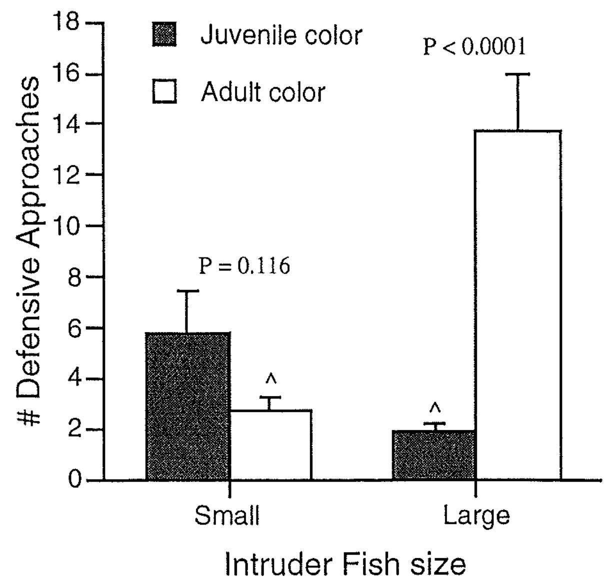

Figure 1. The effects of size and coloration of a damselfish intruder on the # of defenseive approaches by a territorial dusky (mean + SE). P values derived from orthogonal contrasts of the effect of color within each size class (n = 9). ^ indicates that these size and color combinations are models, while the others are live fish.

compared to large models with adult dusky coloration ($F_{1,10} = 2.02$, $p = 0.19$). Among live, small intruders, a one-way ANOVA showed that there was no difference in the response to juvenile dusky versus juvenile threespot coloration ($F_{1,16} = 0.88$, $p = 0.36$). Among intruders with adult dusky coloration, focal fish responded less aggressively to model versus live intruders ($t = 2.265$, $df = 10$, $p = 0.047$). None of the three focal fish given the control treatment showed any response to its presence.

Discussion

My results suggest that juvenile coloration does decrease the degree of territory defense exhibited by the focal fish in response to large intruders, as compared to those with adult coloration. Specifically, both adult size and coloration are required to instigate a strong territorial response. This effect could be because focal fish recognized adults as competitors, and juvenile coloration and size was enough to signal that an intruder was not a threat. This could imply that there is a response of focal fish to adult behavior, which signals stronger intra- and interspecific competition with adults than with juveniles. However, the decreased response to large intruders with juvenile coloration could also indicate that the behavioral stimulus provided by the live fish, which was lacking in the models, initiated more aggressive responses from the focal fish, as indicated by the equal responses to both large models of adult dusky and juvenile dusky coloration.

It is surprising that the focal fish responded no differently to dusky or threespot intruders, regardless of size or color. The species-specific juvenile coloration does not appear to influence the aggressive response of conspecific adults, as shown by the equivalent response to live juvenile dusky and threespot intruders. If the juveniles of these species have the same habitat preferences as adults, which have been shown to differ (Gutierrez 1998), then it does not seem to be beneficial for the dusky adults to expend energy defending their territory from threespot individuals, either adult or juvenile. However, my study was conducted at a large distance from the reef crest, where the lack of optimal habitat may have increased competition between the species, therefore creating equally high intra- and interspecific competition between adults.

I observed different territory choice between juvenile dusky and threespot damselfish. While all four dusky juveniles were observed alone in the vicinity of conspecific adults, the juvenile threespots were never seen in the area of adult threespots, but were often near adults of other species. These observations could indicate that the coloration of dusky juveniles does deter aggressive responses by conspecific adults, while the coloration of threespot juveniles serves some other purpose.

My results provide evidence that juvenile coloration may reduce dusky response intensity to large intruders, although these results could be clouded by model effects. Future studies should further isolate the effect of color by only using models to simulate intruders and by extending the scope of this study to other damselfish species. The dichromatic lifestages could explain the evolution of behavior within these species that allows them to maintain their niches in coral reef ecosystems at limited costs to both juveniles and adults.

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